

AN EXPERIMENTAL STUDY OF NEST PREDATION IN A SUBTROPICAL WET FOREST FOLLOWING HURRICANE DISTURBANCE

STEVEN C. LATTA¹, JOSEPH M. WUNDERLE, JR.¹, ESTEBAN TERRANOVA,¹
AND MICHELLE PAGÁN²

ABSTRACT.—We used artificial nest experiments to study rates and patterns of egg predation in subtropical wet and lower montane wet forest on the island of Puerto Rico. Levels of depredation were higher for ground nests than for elevated nests, but we found no difference in rates of egg predation between forest edge (5–50 m) and forest interior (100–250 m) nests. We quantified 25 forest vegetation variables surrounding ground and elevated, forest interior nests, and correlated nest success with these vegetation parameters. Utilizing discriminant function analysis, nest success was correctly classified in 59% of cases (for ground nests) using two vegetation variables (shrub density and vegetation in the 2.5–3.0 m foliage height class), and in 71% of cases (for elevated nests) using six vegetation variables (canopy cover, vegetation in the 0–0.5, 0.5–1.0, 1.0–1.5, and 3.0–4.0 m foliage height classes, and *Cecropia* tree density). Our data suggest that the absence of an induced edge effect is the result of the creation of canopy openings and early successional vegetative associations in a matrix across the forest following hurricane disturbance in 1989. Comparative data suggest that the high rates of egg predation recorded here may be typical for insular forest habitats. Received 21 Oct. 1994, accepted 15 May 1995.

SINÓPSIS.—Usamos la experimentación con nidos artificiales para estudiar las razones y patrones de la depredación de los huevos en un Bosque Subtropical Húmedo y en un Bosque Montañoso Bajo Húmedo en la isla de Puerto Rico. Los niveles de depredación fueron mayores en los nidos puestos en el suelo que aquellos que estaban elevados, pero no encontramos diferencias en la razón de depredación entre los nidos que estaban en el linde del bosque (5–50 m) o en el interior (100–250 m). Cuantificamos 25 variables de la vegetación en los nidos del interior del bosque -elevados y en el suelo- correlacionando el éxito del nido con estos parámetros de vegetación. Utilizando un análisis de función discriminante, el éxito del nido fue correctamente clasificado en el 59% de los casos (para los nidos en el suelo) usando dos variables (la densidad de arbustos y la vegetación en la clase de altura de 2.5–3.0 m), y en un 71% de los casos (para los elevados) usando seis variables (la cobertura del dosel, la vegetación en las clases de altura de 0–0.5, 0.5–1.0, 1.0–1.5, y 3.0–4.0 m, y la densidad de *Cecropia*). Nuestra data sugiere que la ausencia de un efecto inducido por el borde del bosque es el resultado de la creación de aberturas en el dosel y de tempranas asociaciones sucesionales de la vegetación en una matriz a través del bosque luego de las alteraciones causadas por un huracán en 1989. Data comparativa sugiere que los altos grados de depredación registrados aquí pudieran ser típicos de los hábitats de bosques insulares.

Forest edges have negative impacts on a diversity of forest interior bird species (reviewed in Yahner 1988, Paton 1994). This is particularly evi-

¹ International Institute of Tropical Forestry, U.S.D.A. Forest Service, P.O. Box B, Palmer, Puerto Rico 00721.

² Dept. of Biology, Univ. of Puerto Rico, Río Piedras, Puerto Rico 00931.

dent in experiments using baited artificial nests which have shown a positive correlation between egg depredation and proximity to the forest edge (Wilcove 1985, Andr n and Angelstam 1988, Berg et al. 1992). Most of these studies have been conducted in the north temperate zone, and only recently have scientists studied the effects of forest edges on nest predation in the tropics. Gibbs (1991) demonstrated an association between nest loss and type of forest edge, with elevated nest loss observed at forest/second-growth edges, but not at forest/pasture borders. He speculated that second-growth forest provides more cover and food resources for predators, thus higher levels of animal movement and nest loss may be expected. Most studies at all latitudes have focused on the forest/field ecotone produced through anthropogenic means (induced edges, *sensu* Yahner 1988), and only a few studies relate patterns of egg predation to quantitative measures of vegetation structure (e.g., Kelly 1993, Seitz and Zegers 1993, Thurber et al. 1994). Natural disturbances, however, such as blowdowns, tree-falls, and fire, may also produce forest edges (inherent edges, *sensu* Yahner 1988), resulting in forest fragmentation and regeneration with a mosaic quality. In the Caribbean, hurricanes are a major factor in shaping forest vegetation structure, often resulting in patchy damage that affects forest stand structure and dynamics for decades (Brokaw and Grear 1991, Brokaw and Walker 1991).

In this study we used artificial nests (*cf* Wilcove 1985) to examine nest predation in subtropical wet, and lower montane wet forest in Puerto Rico. Our purpose was to assess patterns of nest predation across a hurricane damaged forest landscape. We compared loss of ground and elevated nests in forest edge habitats to that in forest interior sites at a range of distances from the induced forest edge. Additionally, we quantified forest vegetation and structure at 59 forest interior nest sites and related patterns of nest predation to these variables.

STUDY AREA AND METHODS

Field work was conducted during the songbird nesting season from 29 April–26 May 1993 in the Luquillo Experimental Forest (LEF, also known as Caribbean National Forest), Puerto Rico. The LEF encompasses 11,500 ha and includes four major vegetation associations (Ewel and Whitmore 1973) that are altitudinally stratified. These are the tabonuco, or subtropical wet forest (200–600 m), palo colorado, or lower montane wet forest (600–900 m), palm forest or brake (>600 m), and the cloud forest (>850 m) (Brown et al. 1983). Portions of the forest were damaged by Hurricane Hugo in September 1989 (Walker et al. 1991).

In most trials we used straw-colored wicker (split bamboo), open-cup nests measuring 100 mm (diameter) by 60 mm (depth) obtained from pet supply stores. Predation rates have been shown to vary with differences in artificial nest appearance (Martin 1987) and with 'real' nests (*i.e.*, unmanipulated nests built by and attended by birds) (Martin 1987, Willebrand and Marcstr m 1988). Therefore, we compared predation levels between artificial

nests and 'natural' nests. Our natural nests were fashioned from abandoned Bananaquit (*Coereba flaveola*) nests. Although these are typically domed nests, they were easily rearranged into a cup-shaped nest.

In all experiments nests were baited with two fresh Japanese quail (*Coturnix coturnix*) eggs (cf Wilcove 1985). We placed nests at the base of trees with the cup nested in the ground (ground nests), and 1.5–2.0 m above the ground in trees or saplings (elevated nests). Elevated nests generally were wedged in forked or trifurcated branches, 0.5–1.0 m from the tree trunk, and sometimes were stabilized with a light gauge wire hanger assembly provided with the nest. Highly exposed nest sites were avoided but no other measures were utilized to conceal the nests or eggs. In all trials forest edge was defined by a paved, two lane highway with 5–10 m wide mowed shoulders. To minimize possible phenological influences, all nests within each trial were placed on the same day or on two consecutive days. Nests were checked in an initial trial every other day for signs of predation until at least 50% of all nests had been depredated. A nest was considered depredated if one or both eggs were found broken or missing. We used these results to redefine our protocol so that in later trials we only visited the nest sites once at the conclusion of the trial. In these trials nests were considered successful if both eggs survived to day six.

The manner of egg depredation was noted as evidence of a predator's identity. Potential nest predators included the exotic species, domestic dog, feral cat, Indian mongoose (*Herpestes auropunctatus*), and black rat (*Rattus rattus*), and the native Pearly-eyed Thrasher (*Margarops fuscatus*), Puerto Rican boa (*Epicrates inornatus*), and the land crab (*Epilobocera sinuatifrons*).

We conducted three sets of experiments. We tested the null hypothesis that there is no difference between predation rates on artificial and natural nests. Twelve elevated nests of each nest type were baited and placed at alternate stations at 50 m intervals along a transect 25 m from and parallel to the forest edge. All nests were placed in tabonuco forest. After six days the number of depredated nests of each type was recorded. A second trial tested the hypotheses that nest success decreases near induced forest edges, and that ground nests are depredated at a higher rate than elevated nests. We set ten transects perpendicular to the induced forest edge in the tabonuco forest (270–560 m). Along each transect six distances were marked at 5 m, 25 m, 50 m, 100 m, 150 m, and 250 m. At each of these stations, two baited, artificial nests were placed (one elevated and one ground) at least 10 m apart. After six days the nests were revisited and signs of depredation recorded. Finally we tested the hypothesis that nest patch (sensu Kelly 1993) vegetation characteristics are correlated with predation rates. Fifty-nine stations were located along four transects which traversed a mosaic of hurricane damaged and relatively undamaged tabonuco and palo colorado forest. In all cases nest sites were located 30 m from a narrow foot trail, 200 m from the next nearest nest site, and a minimum of 250 m from the nearest induced forest edge. At each station we placed two artificial nests (one elevated and one ground) at least 10 m apart. After six days the nests were revisited and signs of depredation recorded.

Nest patch characteristics were estimated within a radius of 11.1 m (0.04 ha) of the nest site, with sampling transects extending in cardinal compass directions from the nest site to the perimeter of the patch. At each plot the following characteristics of the vegetation structure were quantified: (1) Canopy cover was estimated at five points at 1.6 m intervals along the north, south, east and west radii of the circular plot. An ocular tube was used to record the percentage of green vegetation in the canopy at each point (sensu Winkworth and Goodall 1962) and then the mean canopy cover present at these 20 points was calculated. (2) Canopy height was calculated as the mean of the heights of the ten tallest trees in the nest patch as measured with a rangefinder. (3) Maximum canopy height was similarly measured as the height of the tallest tree in the plot. (4) Shrub density was measured as the

TABLE 1
VEGETATION VARIABLES (AND THE CODE USED TO DESCRIBE THEM) USED IN NEST PATCH ANALYSES

Variable code	Variable description
TREE1	Number of trees 3–8 cm dbh
TREE2	Number of trees 8–15 cm dbh
TREE3	Number of trees 15–23 cm dbh
TREE4	Number of trees 23–38 cm dbh
TREE5	Number of trees >38 cm dbh
CANHT	Mean canopy height
MAXHT	Maximum canopy height
SHRUB	Number of woody and herbaceous stems <3.0 cm dbh
COVER	Mean canopy cover
FHC00	Foliage height class 0–0.5 m
FHC01	Foliage height class 0.5–1.0 m
FHC02	Foliage height class 1.0–1.5 m
FHC03	Foliage height class 1.5–2.0 m
FHC04	Foliage height class 2.0–2.5 m
FHC05	Foliage height class 2.5–3.0 m
FHC06	Foliage height class 3.0–4.0 m
FHC07	Foliage height class 4.0–6.0 m
FHC08	Foliage height class 6.0–8.0 m
FHC09	Foliage height class 8.0–10.0 m
FHC10	Foliage height class 10.0–12.0 m
FHC11	Foliage height class 12.0–15.0 m
FHC12	Foliage height class 15.0–20.0 m
CECRO	Percent of total stems identified as <i>Cecropia</i>
TIPUP	Percent of total stems with exposed root wads (tip-ups)
DEAD	Percent of total stems which are dead

number of woody or herbaceous stems <3.0 cm dbh (diameter at breast height) present within 1 m of each transect. (5) All trees >3.0 cm dbh in the nest patch were counted and placed into one of five size classes. Size classes were 3–8 cm, 8–15 cm, 15–23 cm, 23–38 cm, and >38 cm. (6) A foliage height profile was determined for each nest patch by recording the presence of vegetation touches on a tube raised vertically 3.0 m into the canopy. Touches beyond 3.0 m were estimated. Measurements were taken at five points at 1.6 m intervals along each of the four cardinal radii (20 points total). The presence of touches was recorded at height classes: 0–0.5 m, 0.5–1.0 m, 1.0–1.5 m, 1.5–2.0 m, 2.0–2.5 m, 2.5–3.0 m, 3.0–4.0 m, 4.0–6.0 m, 6.0–8.0 m, 8.0–10.0 m, 10.0–12.0 m, 12.0–15.0 m, and 15.0–20.0 m. (7) The number of *Cecropia shreberiana* stems were counted and expressed as a percentage of the total stems in the plot ($[\text{Cecropia stems}/\text{total stems}] \times 100$). (8) Exposed root wads or “tip-ups” were counted and recorded as a percentage of the total stems. (9) Finally, we calculated the percentage of trees that were dead (vertical or horizontal, >3.0 cm dbh). These vegetation variables and the codes used to describe them are summarized in Table 1.

We used the software package SYSTAT Version 5.2 (Wilkinson 1992) in all statistical analyses. Where data were not normally distributed non-parametric statistics were used.

Except where otherwise stated, a probability of Type 1 error of 0.05 or less was accepted as significant but we show greater values for descriptive purposes.

We tested whether nest success was independent of nest type (artificial or natural), or nest location (ground or elevated) by analyzing depredation levels in a 2×2 contingency table using Yates' correction of a G -test of independence which corrects for small samples (Sokal and Rohlf 1994). The influence of distance from the induced edge on nest success was analyzed in a $R \times C$ test of independence with a G -statistic (Sokal and Rohlf 1994) with results for ground and elevated nests analysed separately. In both cases results from nests placed at each distance (5 m, 25 m, 50 m, 100 m, 150 m, 250 m) were first tested separately. We were unable to reject the null hypothesis of independence between nest success and distance from the edge, so we then pooled observations at 5–50 m and 100–250 m in order to increase the number of observations per cell. This was justified by Paton's (1994) observation that the most conclusive studies suggest that edge effects usually occur within 50 m of an edge. We then used a G -test of independence with Yates' correction for continuity to test whether nest success was independent of distance from edge.

Signs suggesting method of egg loss were recorded from 42 depredated ground nests and 24 depredated elevated nests at forest interior nest sites. Observations were placed into one of four categories: (1) eggs removed and nest disturbed; (2) eggs removed but nest remains intact; (3) shell fragments remain in intact nest; or (4) rat signs (teeth marks or feces) present. We used a $R \times C$ test of independence to test the null hypothesis that there was no difference in types of egg depredation between ground and elevated nests.

In the final trial nest success was correlated with vegetation characteristics surrounding nest sites in interior forest. Ground and elevated nests were again analyzed separately. Pearson product-moment correlation coefficients were calculated for all pairwise comparisons of vegetation variables. We then eliminated from subsequent analyses three variables which were found to be highly correlated ($r > 0.70$) with other measures of vegetation structure: maximum canopy height (correlated with mean canopy height), foliage height class 2.0–2.5 m (correlated with foliage height classes 1.5–2.0 m and 2.5–3.0 m), and foliage height class 12–15 m (correlated with foliage height classes 10–12 m and 15–20 m) were eliminated.

Each remaining vegetation variable was then analyzed using an independent samples t -test (separate variances) with a Bonferroni correction for multiple comparisons to test the equality of the means of each vegetation variable grouped by nest success (depredated or non-depredated). In some cases where the assumption of normality was violated, a Mann-Whitney U -test was also utilized, but in all such cases the results were comparable. Only results from t -tests are reported here as the test is considered robust. Vegetation variables that did not differ significantly ($P > 0.10$) between depredated and non-depredated sites were then eliminated from further analyses.

Multivariate analysis of the six remaining vegetation variables associated with elevated nest success, and the two remaining vegetation variables associated with ground nest success, was performed to determine the relative contribution of each variable. We used a discriminate function analysis (Morrison 1976) to compare the vegetation characteristics surrounding depredated and non-depredated nests. The discriminate function analysis calculates a linear combination of the vegetation variables such that the difference between depredated and non-depredated sites is as large as possible. The linear discriminate function is: $z = \alpha_1 x_1 + \alpha_2 x_2 + \dots + \alpha_p x_p$, where z is the discriminant score for P vegetation variables normalized with a mean of 0 and a standard deviation of 1, α is the weight for the vegetation variable i , and x is the value of vegetation variable i ($i = 1, \dots, P$). The Wilks' Lambda F -statistic was used to test the equality of discriminant scores ($P > 0.10$).

TABLE 2
 PERCENTAGE OF GROUND AND ELEVATED NESTS DEPREDATED AT EACH OF SIX DISTANCES
 FROM THE FOREST EDGE

	Distance from forest edge (m)					
	5 ^a	25 ^a	50 ^a	100 ^b	150 ^b	250 ^b
Ground nests ^c	90%	90%	80%	90%	78%	89%
Elevated nests ^c	50%	50%	70%	60%	44%	56%

^a Treatment contained ten nests.

^b Treatment contained nine nests.

^c Percentage of artificial nests in which one or both eggs were removed or damaged after six days of exposure.

RESULTS

We found that more natural nests than artificial nests were preyed upon ($\chi^2 = 6.042$, $df = 1$, $P = 0.014$). After six days of exposure, eggs in nine of 12 natural nests were depredated while eggs in two of 12 artificial nests were lost. Utilizing artificial nests, levels of depredation were significantly higher ($\chi^2 = 12.024$, $df = 1$, $P = 0.0005$) for ground nests (86% depredated, $N = 58$) than for elevated nests (55% depredated, $N = 58$). But we found no difference in levels of depredation between the edge (5–50 m) and the forest interior (100–250 m; Table 2) for either ground nests or elevated nests (both $\chi^2 = 0.000$, $df = 1$, $P = 1.000$).

After six days of exposure 42 of 59 ground nests and 23 of 59 elevated nests were depredated in forest interior sites. Depredation of ground nests (Table 3) occurred where there was significantly higher shrub density, and a suggestion ($P < 0.10$) of more vegetation in the 2.5–3.0 m foliage height class. Depredation of elevated nests (Table 4) occurred where there was significantly less canopy cover, significantly more vegetation in the 0–0.5 m and 0.5–1.0 m foliage height classes, significantly less vegetation in the 3.0–4.0 m height class, and a significantly lower percentage of *Cecropia* trees in the nest patch. Among elevated nests which were depredated there was also a suggestion ($P < 0.10$) of more vegetation in the 1.0–1.5 m foliage height class.

Fisher's linear discriminant function equation for ground nests is: $z = 0.0156(\text{SHRUB}) + 0.0580(\text{FHC05}) - 1.5854$. Normalized scores produced using the means of depredated and non-depredated nests were 0.2148 and -0.2075 respectively. We used the Wilks' Lambda F -statistic to reject the equality of these discriminant scores ($P = 0.091$). Using this model, counts of shrubs and foliage density in the 2.5–3.0 m height class, successfully distinguished 59% of the sites with depredated and non-depredated ground nests in the forest interior.

Fisher's linear discriminant function equation for elevated nests is: $z =$

TABLE 3
COMPARISON OF MEAN (STANDARD ERROR) VALUES OF VEGETATION PARAMETERS
SURROUNDING DEPREDATED AND NON-DEPREDATED GROUND NESTS

Vegetation variable ^a	Depredated	Non-depredated	<i>P</i> ^b
TREE1	39.38 (2.90)	32.18 (3.32)	0.110
TREE2	10.69 (0.94)	84.7 (1.16)	0.706
TREE3	15.31 (1.04)	14.35 (2.27)	0.145
TREE4	4.48 (0.44)	3.59 (0.55)	0.214
TREE5	2.33 (0.32)	2.18 (0.45)	0.778
CANHT	10.24 (0.36)	10.43 (0.85)	0.838
SHRUB	95.83 (5.72)	73.23 (7.89)	0.027
COVER	86.31 (2.04)	84.41 (5.03)	0.730
FHC00	16.00 (0.46)	16.47 (0.68)	0.572
FHC01	9.26 (0.57)	9.76 (1.42)	0.746
FHC02	7.31 (0.47)	6.71 (1.21)	0.646
FHC03	5.45 (0.53)	6.23 (1.03)	0.507
FHC05	5.26 (0.50)	4.06 (0.50)	0.095
FHC06	9.00 (0.72)	9.12 (1.03)	0.926
FHC07	6.21 (0.52)	5.00 (0.85)	0.232
FHC08	7.00 (0.67)	6.53 (0.95)	0.689
FHC09	5.69 (0.73)	8.18 (1.39)	0.126
FHC10	4.07 (0.72)	5.94 (0.94)	0.122
FHC12	0.40 (0.22)	0.88 (0.45)	0.351
CECRO	6.67 (1.79)	7.53 (2.69)	0.791
TIPUP	0.67 (0.21)	0.53 (0.26)	0.686
DEAD	8.20 (0.74)	6.87 (1.22)	0.361

^a Vegetation variables described in Table 1.

^b *P*-values from independent samples *t*-tests (separate variances) with a Bonferroni correction for multiple comparisons based on 59 forest-interior nests.

$-0.0127(\text{COVER}) + 0.0116(\text{FHC00}) + 0.1194(\text{FHC01}) + 0.0868(\text{FHC02}) - 0.0946(\text{FHC06}) - 7.1382(\text{CECRO}) + 0.3434$. Normalized scores produced using the means of depredated and non-depredated nests were 0.7364 and -0.0974 respectively. We rejected the equality of these scores using the Wilks' Lambda test statistic ($P = 0.010$). Using this model, success of forest interior elevated nests was correctly classified by these six vegetation variables in 71% of cases.

The absolute value of the linear correlation of each vegetation variable with the discriminant function was calculated for ground nests (SHRUB, $r = 0.97$; FHC05, $r = 0.62$) and for elevated nests (COVER, $r = 0.52$; FHC00, $r = 0.43$; FHC01, $r = 0.64$; FHC02, $r = 0.42$; FHC06, $r = 0.47$; CECRO, $r = 0.60$). These correlations are a relative indication of the strength of the specific vegetation variable to discriminate between depredated and non-depredated nests in the discriminant function equation.

TABLE 4
COMPARISON OF MEAN (STANDARD ERROR) VALUES OF VEGETATION PARAMETERS
SURROUNDING DEPREDATED AND NON-DEPREDATED ELEVATED NESTS

Vegetation variable ^a	Depredated	Non-depredated	P ^b
TREE1	32.70 (3.61)	40.25 (2.92)	0.110
TREE2	13.74 (1.75)	15.86 (1.15)	0.318
TREE3	8.91 (1.07)	10.78 (1.02)	0.213
TREE4	4.00 (0.53)	4.36 (0.47)	0.611
TREE5	2.52 (0.44)	2.14 (0.33)	0.491
CANHT	9.80 (0.46)	10.62 (0.49)	0.232
SHRUB	86.04 (6.06)	91.42 (6.93)	0.562
COVER	80.00 (4.40)	89.44 (1.57)	0.053
FHC00	17.04 (0.54)	15.55 (0.50)	0.050
FHC01	11.35 (0.95)	8.17 (0.63)	0.008
FHC02	8.26 (0.75)	6.42 (0.59)	0.060
FHC03	6.09 (0.78)	5.42 (0.61)	0.501
FHC05	4.78 (0.75)	5.00 (0.43)	0.803
FHC06	7.52 (0.91)	10.00 (0.72)	0.039
FHC07	5.87 (0.76)	5.86 (0.55)	0.993
FHC08	6.83 (0.86)	6.89 (0.72)	0.956
FHC09	6.39 (0.96)	6.42 (0.91)	0.985
FHC10	4.39 (0.95)	4.75 (0.75)	0.769
FHC12	0.78 (0.40)	0.39 (0.21)	0.388
CECRO	2.09 (1.16)	10.00 (2.17)	0.002
TIPUP	0.87 (0.26)	0.47 (0.22)	0.251
DEAD	6.97 (0.80)	8.35 (0.90)	0.260

^a Vegetation variables described in Table 1.

^b P-values from independent samples *t*-tests (separate variances) with a Bonferroni correction for multiple comparisons based on 59 forest-interior nests.

Ground and elevated nests showed different patterns of depredation ($\chi^2 = 17.981$, $df = 3$, $P = 0.001$). Eggs disappeared in 67% of the depredated ground nests ($N = 42$) and in 42% of the depredated elevated nests ($N = 24$). Shell fragments were found in 19% of depredated ground nests ($N = 42$), and in 42% of depredated elevated nests ($N = 24$). Two percent of ground nests ($N = 42$) showed signs of rat presence, as did 8% of the elevated nests ($N = 24$). Displacement or nest destruction was found in 12% of the depredated ground nests ($N = 42$) and 8% of the depredated elevated nests ($N = 24$).

DISCUSSION

In studies in the northern temperate zone, Martin (1987) has shown a poor correlation between predation rates on artificial and natural nests and warned against overgeneralizing results based on artificial nest studies

alone. Our results show higher predation on natural nests, the first reported from a tropical forest, indicating that the levels of predation we recorded on artificial nests may underestimate actual predation levels. These data suggest that the proportion of nests lost cannot be translated to actual predation rates on 'real' nests, and should be used only as a means of answering comparative questions of rates of predation in different habitats (Seitz and Zegers 1993) and under different conditions.

We found ground nests to have higher rates of depredation than elevated nests, and this is consistent with many previous studies in a variety of habitats (Loiselle and Hoppes 1983; Wilcove 1985; Yahner and Scott 1988; but see Martin 1992a, b; Seitz and Zegers 1993). This difference is likely the result of the relative abundance and influence of terrestrial, mammalian predators as opposed to avian or mammalian arboreal predators, and the influence of habitat and vegetation characteristics in concealing predators or nests (see below).

The absence of a relation between nest predation and distance from a road was unexpected for several reasons. First, roads have been used in previous studies to define edges (Boag et al. 1984) and have negatively affected nest success (Yahner 1988). Second, many ecological effects of roads have been noted, including their use as corridors by predatory corvids (Angelstam 1986), and by dogs, cats, and Pearly-eyed Thrashers in the LEF (J. Wunderle, pers. obs.), and an increase in edge-related passerines (Wunderle et al. 1987). Furthermore, roads frequently increase the incidence of landslides, contributing to the availability of disturbed sites which may serve as stepping stones or corridors for invasion of the forest by exotic species.

A likely explanation for our failure to find a positive relationship between nest success and distance from the forest edge is that predatory edge specialists are responding not only to the induced forest edge (the road) but to inherent forest edges and the natural heterogeneity in vegetation throughout this tropical forest. We suggest that our results reflect a continuing effect of Hurricane Hugo on nest predation 3½ years after the passage of the storm.

The passage of Hurricane Hugo resulted in a radical change in the physical structure of the forest (Brokaw and Walker 1991) resulting from defoliation and the uprooting and snapping of tree trunks. But the extent of localized damage was affected by topography, stand characteristics, and the properties of individual trees and species (Brokaw and Gear 1991), resulting in a patchwork of damage. Following the hurricane, differential recovery, recruitment, and growth rates contributed to a forest structure in which the disparate damage is expected to be evident for decades (Brokaw and Walker 1991). At present, damaged forest is char-

acterized by a more open canopy, the creation of early successional vegetative associations (Brokaw and Walker 1991, Tanner et al. 1991), and the presence of *Cecropia shreberiana* in approximately $\frac{1}{4}$ – $\frac{1}{3}$ of the created openings (D. J. Lodge, unpubl. data).

Our results suggest that egg predation occurred most frequently at both ground and elevated nests in areas damaged by the hurricane, but that differences in the recovery of vegetation also affected the probability of nest success. Among our direct measures of damage (canopy cover, tip-ups, dead stems), only canopy cover was found to differ significantly between depredated and non-depredated, ground or elevated nests. The absence of a relationship of tip-ups or dead stems with depredation may reflect the variety of mortality factors at play in the forest in the years since the hurricane, or this hurricane damage may have been obscured in the recovery process. Changes in canopy closure would be expected to change much less rapidly. Much stronger relationships with nest success were seen in measures of forest recovery, represented by the prevalence of early successional vegetative associations (shrubs; foliage height classes 0–0.5 m, 0.5–1.0 m, 1.0–1.5 m) that respond positively to canopy openings. Another indicator of recovery, *Cecropia* stems, may have obscured some of these vegetative effects because of its patchy distribution, and its ability to shade out the recovery response of some understory species.

Among ground nests we found a positive relationship between shrub density and egg predation and this vegetation variable was very highly correlated with our discriminant function equation. This suggests that predation on ground nests was higher in forest patches where hurricane recovery may be present. Foliage in the 2.5–3.0 m range was only weakly associated ($P < 0.10$) with predation of ground nests and was moderately correlated with the discriminant function. We therefore consider it of minor importance in distinguishing between successful and unsuccessful nest sites.

Among elevated nests, egg predation was associated with nest sites having a more open canopy, and a suite of vegetation characteristics indicating a dense understory. A consistent trend is evident where the lower foliage height classes (0–0.5 m, 0.5–1.0 m, 1.0–1.5 m) are positively related to egg predation, while the mean score for the higher foliage variables (canopy cover, foliage height class 3.0–4.0 m) are negatively associated with egg loss. These data are consistent with the possibility that predation is higher in some areas heavily affected by the hurricane, but where colonization by *Cecropia* has not occurred. Sites with an abundance of *Cecropia* had lower rates of nest predation than sites with few or no *Cecropia*. Although *Cecropia* responds to disturbance and would

seem to favor nest predators, we suspect that predators avoid the branchless *Cecropia* and its typically open understory (Martin 1993, Kelly 1993).

We can only speculate on the identities of egg predators. Based on our observations of the modes of predation, we believe that most of the elevated nests were depredated by our only abundant avian predator, the Pearly-eyed Thrasher. The thrasher is known to be a very important source of mortality of eggs of many bird species (Snyder et al. 1987), and commonly breaks the eggs, leaving large jagged fragments in the nest (W. Arendt, pers. comm.). Such fragments were found in 19% of ground nests, but in more than 40% of elevated nests, that were depredated.

Eggs were carried away from most depredated ground nests, as well as many elevated nests. Predators large enough to remove eggs include the Puerto Rico boa, though it is most commonly seen at elevations below 400 m (Snyder et al. 1987), dogs, cats, rats, and the mongoose. Because mongooses are numerous and widespread, we believe that they may be responsible for much of the ground nest depredation, but more data are needed.

We compared predation rates on artificial, open cup nests from this study to those reported from three other tropical, forest-interior sites. Because exposure periods differed, we calculated a daily predation rate, assuming that predation pressure is constant over the duration of each study. Gibbs (1991) reported predation rates of mainland Costa Rican ground nests (3.4%) and elevated nests (1.4%) quite similar to those reported by Loiselle and Hoppes (1983) from their Panamanian mainland site (3.0% for both ground and elevated nests). In contrast, we observed much higher daily predation rates for both ground nests (11.8%) and elevated nests (6.5%) in this insular subtropical forest, as did Loiselle and Hoppes (1983) on Barro Colorado Island (BCI, Panama) (50.0% and 9.5% respectively). As Loiselle and Hoppes (1983) noted, the magnitude of the difference in predation rates between BCI and the mainland is remarkable. Karr (1982) and Gibbs (1991) have suggested that predation at BCI may be unusually high due to an elevated density of nest predators on the recently created (1914) island. Predation rates from this Puerto Rican forest, however, approach those from BCI (particularly for elevated nests) and suggest that the high predation rates from BCI may not be an anomaly from a unique island, but characteristic of insular forest habitats. While the diversity of predators is undoubtedly lower in island habitats, we suspect that the density of predators may be much higher. Potential predators such as thrashers, rats, and mongooses are all extremely abundant. Caribbean islands are also more prone to disturbance (such as hur-

ricanes; Walker et al. 1991), thus creating habitat that is frequently utilized by these same nest predators.

The many effects of hurricanes on birds are well known (reviewed in Wiley and Wunderle 1994), as is the short-term response of bird populations to hurricane damage (Wiley and Wunderle 1994). We present evidence for long-term, increased predation associated with hurricane-induced early successional vegetative associations. The fact that we were unable to identify an induced edge effect may be attributed to the creation of canopy openings and a matrix of inherent edge habitat across the forest (habitat frequently used by nest predators) following the passage of Hurricane Hugo.

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